

Characterization of antennal sensilla of the wood-feeding cockroach *Cryptocercus* (Blattodea: Cryptocercidae): an exploration of taxonomy

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Abstract: Antennal sensilla are investigated in three xylophagous cockroaches: *Cryptocercus meridianus*, *C. habaensis* and *C. changbaiensis*, using scanning electron microscopy (SEM). General morphology of the antenna is provided in detail, and no significant differences are found among the three species. Six primary types of sensilla are observed and measured: sensilla chaetica (Ch), sensilla trichodea (Tr), sensilla basiconica (Ba), sensilla coeloconica (Co), sensilla campaniformia (Ca) and sensilla capitula (Cp). Sensilla trichodea 1 (Tr1) is the most abundant sensillum in all three species. There are some statistical differences between sexes and among species. Comparing *Cryptocercus* with other cockroaches and termites, we briefly discuss the differences among them in terms of their habitat. According to the statistical analysis performed with the sensilla, these morphological characteristics are not enough to separate the three species and may not be suitable for a classification at species level.

Key words: cockroach; antennae; SEM

食木性隐尾蠊属的触角感器特征及分类意义探究（蜚蠊目：隐尾蠊科）

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摘要：利用扫描电镜观察了3种食木性蜚蠊：滇南隐尾蠊、哈巴隐尾蠊和长白隐尾蠊的触角感器。在本文中对上述3种隐尾蠊的触角形态进行了详细的描述，3种隐尾蠊触角无明显差异。观察并测量了6种主要的感器类型：刺形感器、毛形感器、锥形感器、腔锥形感器、钟形感器和小头感器。结果发现，在3种隐尾蠊触角上毛形感器是最丰富的感器。统计表明感器在3种隐尾蠊种间和两性间存在一些差异。与其他蜚蠊和白蚁进行了比较，并讨论了它们在生活习性上的差异。综上所述，感器的形态描述和统计分析不足以对3种隐尾蠊进行分类鉴别，不宜作为种级单元分类特征。

关键词：蜚蠊；触角；扫描电镜

Introduction

The genus *Cryptocercus* Scudder is a group of wood-feeding cockroaches including 31

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species, distributed in East Asia and North America (Wang *et al.* 2015; Che *et al.* 2016; Bai *et al.* 2018). They are recorded in temperate woodlands, live in and feed on moist logs for their entire life, and are known for subsociality and parental care (Ritter 1964; Seelinger & Seelinger 1983; Nalepa 1984, 2003; Park *et al.* 2002). *Cryptocercus* is now considered to be the sister group to termites, occupying an important phylogenetic position in the Blattodea (Lo *et al.* 2000, 2006, 2007; Klass & Meier 2006; Inward *et al.* 2007; Ware *et al.* 2008; Cameron *et al.* 2012).

The antennae of insects with dense sensilla play an important role during their entire lifetime (Schneider 1964). For example, the sensilla chaetica in *Chlorophorus caragana* (Schneider 1964), the bristles in *Rhodnius* (McIver & Siemicki 1984), and the basiconic sensilla in the damp-wood termite *Hodotermopsis sjostedti* (Ishikawa *et al.* 2007) all act as mechanosensitive sensilla. Sensilla basiconica have been considered chemoreceptors in the bird louse and human louse (Slifer 1976; Slifer & Sekhon 1980). Sensilla chaetica, trichodea and basiconica in *Coptotermes formosanus* act as tactile mechano-, olfactory- and chemoreceptors, respectively (Tarumingkeng *et al.* 1976; Yanagawa *et al.* 2009; Yanagawa *et al.* 2015). The characteristics of antennal sensilla can be observed through scanning electron microscopy and have become an approach to taxonomic comparison between genera and species. Sensillum type, number, length and distribution, employed as the main characters in taxonomy, are successfully used in Muscidae, Triatominae, *Anopheles* and *Yponomeuta* (Cuperus *et al.* 1983; Gracco & Catalá 2000; Carrico *et al.* 2015; Hempolchom *et al.* 2017). Conversely, sensillar morphology is not a useful tool for Philanthinae taxonomy (Polidori *et al.* 2012).

The morphology of antennal sensilla of cockroaches has been extensively described (*Periplaneta americana*: Schafer & Sanchez 1973, 1976; *Periplaneta brunnea*: Nishino *et al.* 1980; *Leucophaea maderae*: Schafer 1971, 1973; Schaller 1982; *Paratemnopteryx*: Bland *et al.* 1998; etc.). Several common sensillum types were recorded and described in these studies, including sensilla chaetica, sensilla trichodea, sensilla basiconica, sensilla campaniformia, sensilla capitulum and sensilla coeloconica. These sensilla are known as mechano-, chemo-, hygro-, thermo- and olfactory receptors (Schafer 1970; Schafer & Sanchez 1973; Altner *et al.* 1977; Yokohari 1981; Tominaga & Yokohari 1982; Nishikawa *et al.* 1992). In addition, sexual dimorphism was found on the antennal sensilla of *P. americana* (Schafer & Sanchez 1973, 1976). However, for *Cryptocercus*, which is unique in biological habits and phylogenetic position, no information on the antennal sensilla has been reported.

In this paper we have chosen three species that cluster in one lineage in phylogenetic analysis (Bai *et al.* 2018), but their geographical ranges are diverse with *C. meridianus* and *C. habaensis* distribute in Yunnan (south China) and *C. changbaiensis* find in Manchuria (northeastern China). The main objective of this report is to provide information on the morphology and distribution of the antennal sensilla in *Cryptocercus* and to test whether antennal sensillum can be used for *Cryptocercus* species identification. We also compare *Cryptocercus* with other cockroaches and termites and discuss the relationships between sensillar characters and species. As a descriptive study, this is a basis for future behavioral analysis.

Material and methods

Insects

The sources of the three species used in this study and the collecting information are listed in Table 1. Six adults of each species were studied, including three males and three females each. All specimens are deposited in the Institute of Entomology, Southwest University (SWU), Chongqing, China.

Scanning electron microscopy (SEM)

The antennae were removed from the base of the scape with fine scissors. The preparation procedure for SEM was as follows: (1) fixing with 2.5% glutaraldehyde for 2h at room temperature; (2) rinsing 3 times (10 min/time) with phosphate-buffered saline (PBS, pH 7.2); (3) rinsing with deionized water (3 times, 10 min/time); (4) cleaning in an ultrasonic bath (4 times, 5 min/time); (5) dehydrating in a graded ethanol series (1 time for 10 min each with 60%, 70%, 80%, 90%; 2 times at 10 min with 100% ethanol); (6) drying for 12h at room temperature; (7) mounting on the platform using double-sided adhesive tape; (8) sputter-coating with gold in a Hitachi E-1010 high resolution sputter coater; and (9) observing with a Hitachi S-3000N SEM (Hitachi Corp., Tokyo, Japan) at 20 kV.

Table 1. Collecting data for the *Cryptocercus* specimens used in this study.

Species	Locality	Collecting date	Preservation	Voucher
<i>C. meridianus</i>	Yunshanping (3250m),	18-VII-2012		1.1–1.3 Female
	Yulongxueshan, Lijiang, Yunnan	07-V-2016		1.4–1.6 Male
<i>C. habaensis</i>	Habaxueshan (3126m), Shangri-la,	16-X-2014	absolute	2.1–2.3 Female
	Diqing, Yunnan	09-V-2016	ethanol	2.4–2.6 Male
<i>C. changbaiensis</i>	Changbaishan (750m), Baishan, Jilin	06-VIII-2015		3.1–3.3 Female
		01-VII-2016		3.4–3.6 Male

Data analysis

Classification and characterization of the sensilla follows Schneider (1964). Samples of the antennae were taken from the 18th through 20th segments, because the 15th or 16th proximal segments are called meristal segments and possess fewer sensilla than distal segments (Schafer & Sanchez 1973). The sensilla were identified, measured and counted in the SEM micrographs. The Tukey test was used to compare antennae and sensilla data for the three species (SPSS Statistics V22.0 for Windows, $P < 0.05$).

Results

General morphology

In the three species, each antenna consists of a basal scape, a cylindrical pedicel and a filiform-like flagellum, with different flagellar segments (Figs. 1A–C; Table 2). The scape is longer than the pedicel. The flagellar segments are of various sizes, especially the proximal ten segments which are shorter than the others (Fig. 1A). The 11th through 20th segments are stubby, and the distal ones are slightly slender. Cuticles of the scape and pedicel are relatively

smooth, but those of the meristal segments bear some squamae. Tapered protuberances are densely distributed on the rest of the flagellar segments (Figs. 1B–F). These protuberances are present in the fifth through tenth flagellar segments, and gradually increase in number from the proximal to the distal end of each segment. The lengths of these protuberances are $5.63 \pm 1.43 \mu\text{m}$ ($n = 20$). In all three species, epidermal gland pores open onto the surface of the cuticle (Fig. 3A). The antennal apices exhibit some differences among the three species but are unstable or highly varied. From the characteristics mentioned above, we can see that the three species are extremely similar in general antennal morphology.

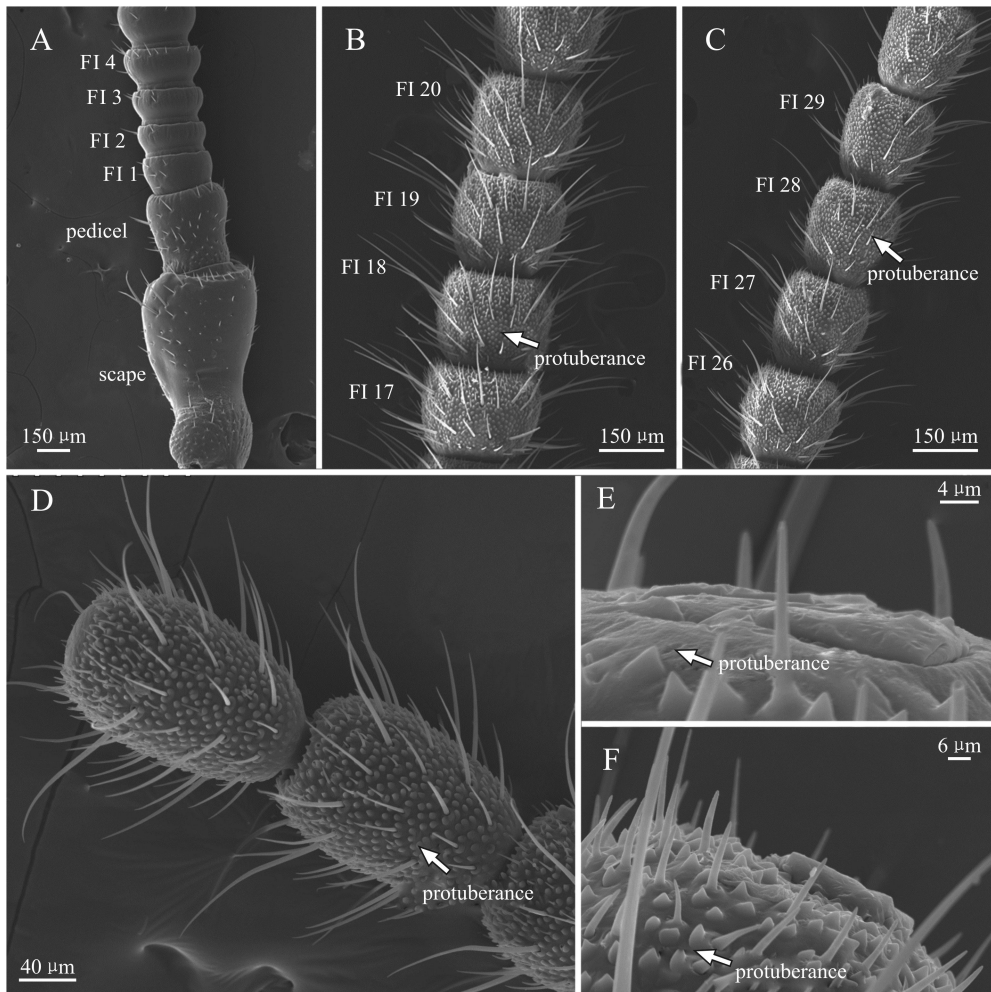


Figure 1. The segments of antennae. A. Proximal segments of *C. meridianus*; B. Middle segments of *C. meridianus*; C. Distal segments of *C. meridianus*; D. Antennal terminal segments of *C. habaensis*; E. Antennal apex of *C. meridianus*; F. Antennal apex of *C. changbaiensis*. Abbr.: FI—flagellar segment.

Table 2. Average dimensions, flagellar segments, and sensilla number/segment for the antennae (mean \pm SD).

Species	Length (mm)	Diameter (μ m)	Segments	Ave. sensilla number
<i>C. meridianus</i>				
Male	7.57 \pm 0.95a	247.86 \pm 16.68a	39 \pm 5.57a	147.11 \pm 15.32a
Female	7 \pm 0.95a	228.17 \pm 49.21a	38 \pm 6.93a	141.56 \pm 28.50a
<i>C. habaensis</i>				
Male	7.67 \pm 0.21a	231.79 \pm 11.65a	37 \pm 5.29a	140.78 \pm 21.31a
Female	7.63 \pm 0.49a	243.66 \pm 24.42a	35 \pm 2.65a	156.89 \pm 30.72a
<i>C. changbaiensis</i>				
Male	6.83 \pm 0.29a	256.80 \pm 26.37a	30 \pm 3.46a	144 \pm 26.25a
Female	7 \pm 1.3a	228.63 \pm 13.55a	32 \pm 7.57a	149.44 \pm 32.2a

Same letter in the same line indicates no significant differences were found among the three species (Tukey test, $P < 0.05$).

Types and characteristics of sensilla

Six primary morphological types of sensilla were observed among the three species. They have the same sensillum types with common morphologies. They are recognized as sensilla chaetica (Ch1, Ch2, Ch3), sensilla trichodea (Tr1, Tr2), sensilla basiconica (Ba1, Ba2), sensilla coeloconica (Co), sensilla campaniformia (Ca), and sensilla capitula (Cp). From the scape to the last flagellar segment, the number and types of sensilla gradually increased in all three species. The six main sensillum types occur in the same longitudinal pattern among species and between sexes but the distribution of each sensillum type is different (Table 3).

Table 3. Distribution and function of sensilla for the three species.

Sensilla type	Location and distribution	Function
Ch1	Occur on flagella, approximately starting from seventh, arranged in two rings at distal and proximal margin.	Tactile mechanoreceptors and contact chemoreceptors (Schafer 1970)
Ch2	Occur from scape to the last flagellar segments, irregularly scattered distribution on all segments.	Tactile mechanoreceptors and contact chemoreceptors (Schafer 1970)
Ch3	Occur as hair plate sensilla, four at head-scape and three at scape-pedicel articulations.	Proprioceptors (Schafer 1970)
Tr1	Occur from proximal to distal of flagellar segments, gradually increasing, most abundant at the distal margin.	Chemoreceptors or sensory hairs (Schafer and Sanchez 1973)
Tr2	Occur starting at middle flagellar segments, concentrated in distal margin of some segments.	Chemoreceptors or sensory hairs (Schafer 1971); Olfactory receptors (Schafer 1970)
Ba1	Occur at the distal edge of flagellar segments, grouped with Tr1 from 13 to 15 onward.	Chemo-, hygro-, and thermoreceptors (Altner <i>et al.</i> 1977)
Ba2	Occur always on the distal flagellar segments, a few distributed proximally, generally scattered on the rear with other types.	Chemoreceptors (Altner <i>et al.</i> 1977)

Continued Table 3

Sensilla type	Location and distribution	Function
Co	Occur primarily on scape and pedicel, a few found on proximal mersital segments.	Cold receptors (Loftus 1968); Thermoreceptors (Schafer 1970)
Ca	Occur on flagellar segments in a small amount, separately, annular around the distal edge of the pedicel, a few combined with hair plates.	Mechanoreceptors (Schafer 1970)
Cp	Occur at distal margin adjacent to next flagellum, surrounded by ST I.	Hygro- and thermoreceptors (Yokohari 1981; Tominaga and Yokohari 1982; Nishikawa <i>et al.</i> 1992)

Abbreviations: Ch1–sensilla chaetica 1; Ch2–sensilla chaetica 2; Ch3–sensilla chaetica 3; Tr1–sensilla trichodea 1; Tr2–sensilla trichodea 2; Ba1–sensilla basiconica 1; Ba2–sensilla basiconica 2; Co–sensilla coeloconica; Ca–sensilla campaniformia; Cp–sensilla capitula.

Numerous bristles, sensilla chaetica (Ch), occur on each segment in rows. These sensilla fall into three groups based on their length, namely Ch1, Ch2, and Ch3. Ch1 are long (50 μm and above) (Fig. 2A). Ch2 are shorter than Ch1 (1–49 μm), and are generally located in the distal flagellar segments and scattered on the antennal surface (Fig. 2B). The Ch3 are very short and only located in the distal cuticle of the scape and the pedicel (Fig. 2C).

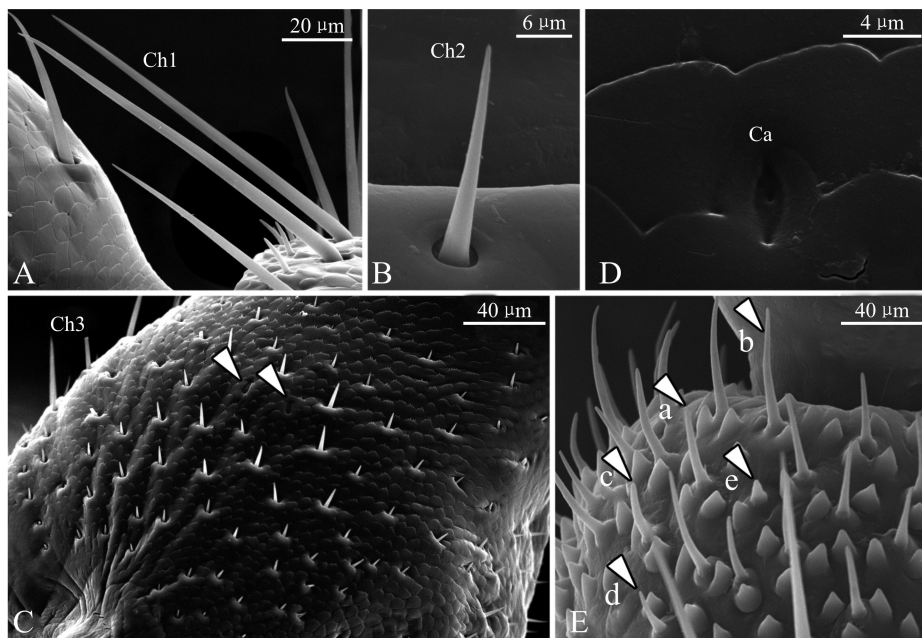


Figure 2. A. Sensilla chaetica 1 (Ch1) of a female *C. habaensis*; B. Sensillum chaetica 2 (Ch2) of a female *C. meridianus*; C. Sensilla chaetica 3 (Ch3), on the basal scape of a male *C. habaensis* and two sensilla campaniformia (Ca) (white triangle); D. A sensillum campaniformum (Ca) of a male *C. habaensis*; E. Distal part of twentieth flagellar segment of a male *C. meridianus* showing (a) sensillum trichodea 1 (Tr1), (b) sensillum trichodea 2 (Tr2), (c) sensillum basiconica 1 (Ba1), (d) sensillum basiconica 2 (Ba2) and (e) sensillum capitulum (Cp).

Sensilla campaniformia (Ca) are rare and always occur on the flagellar segments along the distal edge of the pedicel, and with a few combined with hair plates. There is a pore at the center of each Ca that bears oval cuticle (Fig. 2D).

Sensilla coeloconica (Co) are rare and occur on the scape, pedicel and partial meristal segments. Co are peg-in-pit and vary in length (Fig. 3B).

According to the shape, length and quantity, sensilla trichodea (Tr) can be classified into two types, Tr1 and Tr2. Tr1 are shorter than Tr2 (Figs. 2E (a), 3D and 3E). They occur throughout flagellar segments and gradually increase in number distad; most of them are located in the middle to distal part of each segment (Table 3). Tr2 are very slender and only occur from the 16th to the distal flagellar segments (Figs. 2E (b) and 3D).

Two morphological types of sensilla basiconica (Ba) are identified. Ba1 are similar to trichoid hairs (Tr1) (Figs. 2E(c) and 3C) and they occur from the 13th to 15th segments together with Tr1 onward (Table 3). Ba2 are only scattered at the end of each flagellar segment (Figs. 2E (d), 3D and 3E).

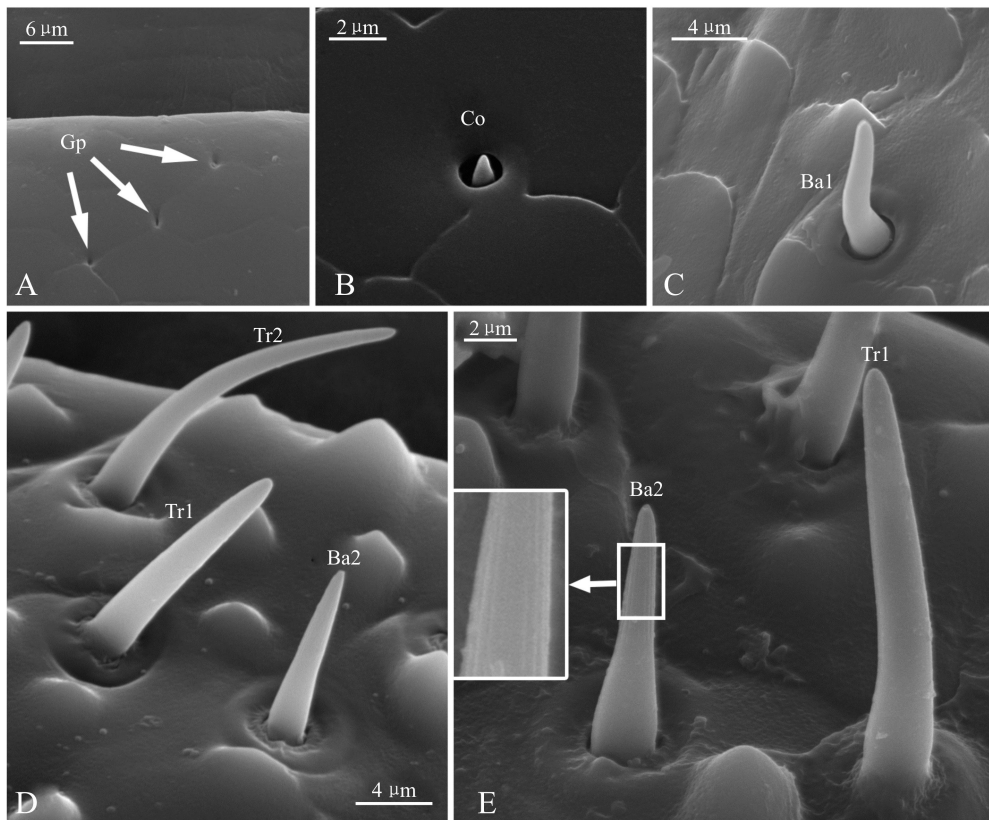


Figure 3. A. Distal part of the fifth flagellar segment of the female *C. meridianus* showing three gland pores (Gp); B. Sensillum coeloconica (Co) of the male *C. habaensis*; C. Sensillum basiconica I (Ba1) of the male *C. meridianus*; D. Distal part of eighth flagellar segment of the female *C. habaensis* showing sensillum trichodea 1 (Tr1), sensillum trichodea 2 (Tr2), sensillum basiconica 2 (Ba2); E. Distal part of eighteenth flagellar segment of the female *C. meridianus* showing sensillum trichodea 1 (Tr1) and sensillum basiconica 2 (Ba2).

Sensilla capitula (Cp) have smooth surfaces and distinctive caps. They always occur at the distal part of each flagellar segment and are surrounded by Tr1. They have a smooth basal part and a fixed socket (Fig. 2E (e)).

Statistics

Statistical analyses suggest that the length and segment number of antennae, and the measurements of the three flagellar segments, are not significantly different among the three *Cryptocercus* species (Table 2). Interspecific differences lie in the antennae sensilla (Table 4), but these limited significant differences only occur in the basal diameter of Co and the length of Tr1 between *C. meridianus* and *C. changbaiensis*, and the type Cp is absent in *C. habaensis*. Most antennal sensilla present no significant differences between sexes, but there are some exceptions. In *C. meridianus*, sexual dimorphism is found in the basal diameter of Tr1 and the lengths of Tr1 and Cp; in *C. habaensis*, the differences exist in lengths of Tr1, average number/segment of Tr2 and basal diameters of Co and Cp; in *C. changbaiensis*, there is sexual dimorphism in the basal diameter of Ch1 and the types of Tr2 and Cp.

Discussion

This study provides descriptions of the antennae and sensillae of three *Cryptocercus* species and addresses both sexes. Antennal morphology and sensillum types of *Cryptocercus* are similar to those of other cockroaches, but they have different habits. These sensilla represent the standard morphologies of *Cryptocercus*, and there are fewer differences in measured features and numbers (Table 4). As a result, these differences are not sufficient to diagnose those three species, and that fails to overcome the disadvantages of basing identification on other morphological characters, which also differ very little (Nalepa *et al.* 1997; Burnside *et al.* 1999; Grandcolas *et al.* 2001; Aldrich *et al.* 2004). The antennae of *Cryptocercus* are shorter and bear fewer segments than those of other cockroaches, such as *P. americana* (Schafer & Sanchez 1973, 1976), *P. brunnea* (Nishino *et al.* 1980), *L. maderae* (Schafer 1971, 1973) and *Paratemnopteryx* species (Bland *et al.* 1998, Table 4). The limited space and stable living conditions in their galleries likely contribute to the short antennae of *Cryptocercus*.

Six main sensillum types are held in common between *Cryptocercus* and *Periplaneta* species (*P. americana* and *P. brunnea*) (Schafer & Sanchez 1973, 1976; Nishino *et al.* 1980). These two *Periplaneta* species are common pests in human settlements. These sensilla may contain mechano-, chemo-, thermoreceptors and proprioceptors, as studied by Schafer (1970). Sensilla trichodea, which respond to chemical substances (Nishino *et al.* 1980), are the most abundant sensilla on the antennae of both *Cryptocercus* and *Periplaneta*. Large numbers of sensilla can provide a greater sensitivity to stimuli, and for either cockroach, the wood-feeding and living *Cryptocercus*, or the omnivore and epigeal *Periplaneta*, these pheromone and odor receptors play the most important roles. These different habits may result in the absence of Cp from *P. americana* and *P. brunnea*, and the absence of the marginal sensilla from *Cryptocercus*.

The antennae of *Cryptocercus* bear both similar shape and sensillar distributions to those of the African woodroach *L. maderae* and the cave-dwelling Australian *Paratemnopteryx* species (Schafer 1971; Bland *et al.* 1998), both of which are tropical. In *L. maderae* nine

sensillum types are verified on the antennae, and most are consistent with *Cryptocercus*, except for the Cp. It is noteworthy that *L. maderae* lives in wood and is xylophagous, similar to *Cryptocercus*. However, *Cryptocercus* is distributed in the temperate zone (Nalepa 1984; Park & Choe 2003). In *Paratemnopteryx*, three main sensillum types were recorded. Like those in *Cryptocercus* and *P. americana* (Schafer & Sanchez 1973), sensilla trichodea are the most abundant type in *Paratemnopteryx*. We suggest that in a gallery or a cave in total darkness, similar to the moist wood galleries where *Cryptocercus* live, the chemoreceptors or olfactory sensilla may be more useful for detection. *Paratemnopteryx* can feed on a variety of liquid and solid foods, especially in the dry season (Bland *et al.* 1998). Certain sensillum types, namely Co, Ca and Cp, are rare in cockroach antennae, and even absent from *Paratemnopteryx*; this suggests that these types may have similar functions to the main types.

As mentioned above, sexual dimorphism exhibits in the sensillum types, number and measurements on *Cryptocercus* antennae. For *Periplaneta*, the sexual dimorphism exists in the distribution of contact chemoreceptors and olfactory sensilla, which are related to mating behavior when males receive stimulation from antennal contact (Schafer & Sanchez 1973, 1976). Sexual dimorphism of *Paratemnopteryx* is exhibited in sensilla chaetica, the number of which is greater in males; this suggests that sensilla chaetica are useful for males to find females in darkness (Bland *et al.* 1998). To the contrary, there is no sexual dimorphism present in the antennae of *L. maderae* (Schafer 1971, 1973). In *Cryptocercus*, statistically supportable sexual dimorphism of Tr (length, diameter and number) occurring in all three species may also reflect their different function in releasing and receiving sex pheromones to locate each other in mating behavior.

In recent phylogenetic works, Cryptocercidae and termites have been recovered as sister groups (Lo *et al.* 2000, 2006, 2007; Klass & Meier 2006; Inward *et al.* 2007; Ware *et al.* 2008; Cameron *et al.* 2012). Compared with those of the termite *Coptotermes formosanus*, the antennae of *Cryptocercus* are longer, wider and possess more flagellar segments (Yanagawa *et al.* 2009). On the other hand, the morphology of both the antennae and sensillum types are similar. However, the marginal sensilla have not yet been observed in any *Cryptocercus*. We infer that this difference may reflect their food preference, i.e. *Cryptocercus* only feeds on rotten wood while the termites feed on wood, pecan, and red gum (Morales-Ramos & Rojas 2003).

This study improves our understanding of *Cryptocercus*, the special wood-feeding cockroaches. Statistical analyses suggest the general morphology of the antennae and sensilla are not suitable for classification of these three *Cryptocercus* species. According to the comparisons above, we suggest that the differences in sensilla may be closely related to their common habits rather than their genetic relationship. These sensilla may play a crucial role in the cockroaches' behavior, for which further study is needed.

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References

- Aldrich BT, Zolnerowich G & Kambhampati S. 2004. Interspecific morphological variation in the wood-feeding cockroach, *Cryptocercus* (Dictyoptera: Cryptocercidae). *Arthropod Structure & Development*, 33: 443–451.
- Altner H, Sass H & Altner I. 1977. Relationship between structure and function of antennal chemo-, hygro-, and thermoreceptive sensilla in *Periplaneta americana*. *Cell and Tissue Research*, 176: 389–405.
- Bai QK, Wang LL, Wang ZQ, Lo N & Che YL. 2018. Exploring the diversity of Asian *Cryptocercus* (Blattodea: Cryptocercidae): species delimitation based on chromosome numbers, morphology, and molecular analysis. *Invertebrate Systematics*, 32: 69–91.
- Bland RG, Slaney DP & Weinstein P. 1998. Antennal sensilla on cave species of Australian *Paratemnopteryx*, cockroaches (Blattaria: Blattellidae). *International Journal of Insect Morphology & Embryology*, 27: 83–93.
- Burnside CA, Smith PT & Kambhampati S. 1999. Three new species of the wood roach, *Cryptocercus* (Blattodea: Cryptocercidae), from the eastern United States. *Journal of the Kansas Entomological Society*, 72: 361–378.
- Cameron SL, Lo N, Bourguignon T, Svenson GJ & Evans TA. 2012. A mitochondrial genome phylogeny of termites (Blattodea: Termitidae): robust support for interfamilial relationships and molecular synapomorphies define major clades. *Molecular Phylogenetics and Evolution*, 65: 163–173.
- Carriço C, Mendonça PM, Cortinhas LB, Mallet JRDS & Queiroz MMDC. 2015. Ultrastructural studies of some character of Diptera (Muscidae) of forensically importance. *Acta Tropica*, 142: 96–102.
- Che YL, Wang D, Shi Y, Du XH, Zhao YQ, Lo N & Wang ZQ. 2016. A global molecular phylogeny and timescale of evolution for *Cryptocercus* woodroaches. *Molecular Phylogenetics and Evolution*, 98: 201–209.
- Cuperus PL, Thomas G & Otter CJD. 1983. Interspecific variation and sexual dimorphism of antennal receptor morphology, in European *Yponomeuta*, (Latreille) (Lepidoptera: Yponomeutidae). *International Journal of Insect Morphology & Embryology*, 12: 67–78.
- Grandcolas P, Park YC, Choe JC, Piulachs MD, Bellés X, D'Haese C, Farine JP, Brossut R & Farine JP. 2001. What does *Cryptocercus kyebangensis*, n. sp. (Dictyoptera, Blattaria, Polyphagidae) from Korea reveal about *Cryptocercus* evolution? A study in morphology, molecular phylogeny, and chemistry of tergal glands. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 151: 61–79.
- Gracco M & Catalá S. 2000. Inter-specific and developmental differences on the array of antennal chemoreceptors in four species of Triatominae (Hemiptera: Reduviidae). *Memórias Do Instituto Oswaldo Cruz*, 95: 67–74.
- Hempolchom C, Yasanga T, Wijit A, Taai K, Dedkhad W, Srisuka W, Thongsahuan S, Otsuka Y, Takaoka H & Saeung A. 2017. Scanning electron microscopy of antennal sensilla of the eight *Anopheles* species of the *Hyrceanus* group (Diptera: Culicidae) in Thailand. *Parasitology Research*, 25: 1–11.
- Huang QY, Guan CS, Shen Q, Hu CQ & Zhu BB. 2012. Aggressive behavior and the role of antennal sensillae in the termite *Reticulitermes chinensis* (Isoptera: Rhinotermitidae). *Sociobiology*, 59: 1239–1251.
- Inward DJ, Vogler AP & Eggleton P. 2007. A comprehensive phylogenetic analysis of termites (Isoptera) illuminates key aspects of their evolutionary biology. *Molecular Phylogenetics and Evolution*, 44: 953–967.
- Ishikawa Y, Koshikawa S & Miura T. 2007. Differences in mechanosensory hairs among castes of the damp-wood termite *Hodotermopsis sjostedti* (Isoptera: Termopsidae). *Sociobiology*, 50: 895–907.
- Klass K-D & Meier R. 2006. A phylogenetic analysis of Dictyoptera (Insecta) based on morphological characters. *Entomologische Abhandlungen (Dresden)*, 63: 3–50.

- Lo N, Tokuda G, Watanabe H, Rose H, Slaytor M, Maekawa K, Bandi C & Noda H. 2000. Evidence from multiple gene sequences indicates that termites evolved from wood-feeding cockroaches. *Current Biology*, 10: 801–804.
- Lo N, Luykx P, Santoni R, Beninati T, Bandi C, Casiraghi M, Lu WH, Zakharov EV & Nalepa CA. 2006. Molecular phylogeny of *Cryptocercus* wood-roaches based on mitochondrial COII and 16S sequences, and chromosome numbers in Palearctic representatives. *Zoological Science*, 23: 393–398.
- Lo N, Beninati T, Stone F, Walker J & Sacchi L. 2007. Cockroaches that lack *Blattabacterium* endosymbionts: the phylogenetically divergent genus. *Biology Letters*, 3: 327–330.
- Loftus R. 1968. The response of the antennal cold receptor of *Periplaneta americana* to rapid temperature changes and to steady temperature. *Journal of Comparative Physiology A*, 59: 413–455.
- Morales-Ramos JA & Rojas MG. 2003. Formosan subterranean termite feeding preference as basis for bait matrix development (Isoptera: Rhinotermitidae). *Sociobiology*, 41: 71–79.
- McIver SB, Siemicki R. 1984. Fine structure of antennal mechanosensilla of adult *Rhodnius prolixus* Stal (Hemiptera: Reduviidae). *Journal of Morphology*, 180: 19–28.
- Nalepa CA, Byers G, Bandi C & Sironi M. 1997. Description of *Cryptocercus clevelandi* (Dictyoptera: Cryptocercidae) from the northwestern United States, molecular analysis of bacterial symbionts in its fat body, and notes on biology, distribution, and biogeography. *Annals of the Entomological Society of America*, 90: 416–424.
- Nalepa CA. 1984. Colony composition, protozoan transfer and some life-history characteristics of the woodroach *Cryptocercus punctulatus* Scudder (Dictyoptera: Cryptocercidae). *Behavioral Ecology and Sociobiology*, 14: 273–279.
- Nalepa CA. 2003. Evolution in the genus *Cryptocercus* (Dictyoptera: Cryptocercidae): no evidence of differential adaptation to hosts or elevation. *Biological Journal of Linnean Society*, 80: 223–233.
- Nishikawa M, Yokohari F & Ishibashi T. 1992. Response characteristics of two types of cold receptors on the antennae of the cockroach, *Periplaneta americana* L. *Journal of Comparative Physiology A*, 171: 299–307.
- Nishino C, Kimura R & Takayanagi H. 1980. External appearance of *Periplaneta brunnea* antennae and their electroantennogram responses to odorous compounds. *Agricultural and Biological Chemistry*, 44: 1461–1467.
- Park YC & Choe JC. 2003. Life history and population dynamics of Korean woodroach (*Cryptocercus kyebangensis*) populations. *Animal Cells and Systems*, 7: 111–117.
- Park YC, Grandcolas P & Choe JC. 2002. Colony composition, social behavior and some ecological characteristics of the Korean wood-feeding cockroach (*Cryptocercus kyebangensis*). *Zoological Science*, 19: 1133–1139.
- Polidori C, Jorge GA & Nieves-Aldrey JL. 2012. Antennal sensillar equipment in closely related predatory wasp species (Hymenoptera: Philanthinae) hunting for different prey types. *Comptes Rendus Biologies*, 335: 279–291.
- Ritter Jr H. 1964. Defense of mate and mating chamber in a wood roach. *Science*, 143: 1459–1460.
- Schafer R. 1970. An electrophysiological survey of antennal sense organs in the cockroach, *Leucophaea maderae*. *American Zoologist*, 40: 310.
- Schafer R. 1971. Antennal sense organs of the cockroach, *Leucophaea maderae*. *Journal of Morphology*, 134: 91–104.
- Schafer R. 1973. Postembryonic development in the antenna of the cockroach, *Leucophaea maderae*: growth, regeneration, and the development of the adult pattern of sense organs. *Journal of Experimental Zoology*, 183: 353–363.
- Schafer R & Sanchez TV. 1973. Antennal sensory system of the cockroach, *Periplaneta americana*:

- postembryonic development and morphology of the sense organs. *Journal of Comparative Neurology*, 149: 335–354.
- Schafer R & Sanchez TV. 1976. Nature and development of sex attractant specificity in cockroaches of the genus *Periplaneta*. I. Sexual dimorphism in the distribution of antennal sense organs in five species. *Journal of Morphology*, 149: 139–157.
- Schaller L. 1982. Structural and functional classification of antennal sensilla of the cockroach, *Leucophaea maderae*. *Cell and Tissue Research*, 225: 129–142.
- Schneider D. 1964. Insect antennae. *Annual Review of Entomology*, 9: 103–122.
- Seelinger G & Seelinger U. 1983. On the social organization, alarm and fighting in the primitive cockroach *Cryptocercus punctulatus* Scudder. *Journal of Comparative Ethology*, 61: 315–333.
- Slifer EH. 1976. Sense organs on the antennal flagellum of a bird louse (Mallophaga). *Journal of the New York Entomological Society*, 84: 159–165.
- Slifer EH & Sekhon SS. 1980. Sense organs on the antennal flagellum of the human louse *Pediculus humanus* (Anoplura). *Journal of Morphology*, 164: 161–166.
- Tarumingkeng RC, Coppel HC & Matsumura F. 1976. Morphology and ultrastructure of the antennal chemoreceptors and mechanoreceptors of worker *Coptotermes formosanus* Shiraki. *Cell and Tissue Research*, 173: 173–178.
- Tominaga Y & Yokohari F. 1982. External structure of the sensilla capitulum, a hygro- and thermoreceptive sensilla of the cockroach, *Periplaneta americana*. *Cell and Tissue Research*, 226: 309–318.
- Wang ZQ, Li Y, Che YL & Wang JJ. 2015. The wood-feeding genus *Cryptocercus* (Blattodea: Cryptocercidae), with description of two new species based on female genitalia. *Florida Entomologist*, 98: 260–271.
- Ware JL, Litman J, Klass K-D & Spearman LA. 2008. Relationships among the major lineages of Dictyoptera: the effect of outgroup selection on dictyopteran tree topology. *Systematic Entomology*, 33: 429–450.
- Yanagawa A, Shimizu S, Noma K, Nishikawa M, Kazumasa O & Yokohari F. 2009. Classification and distribution of antennal sensilla of the termite *Coptotermes formosanus* (Isoptera: Rhinotermitidae). *Sociobiology*, 54: 327–349.
- Yanagawa A, Tomoya I, Toshiharu A, Yoshihiro T & Tsuyoshi Y. 2015. Olfactory cues from pathogenic fungus affect the direction of motion of termites, *Coptotermes formosanus*. *Journal of Chemical Ecology*, 41: 1118–1126.
- Yokohari F. 1981. The sensillum capitulum, an antennal hygroreceptive and thermoreceptive sensillum of the cockroach, *Periplaneta americana* L. *Cell and Tissue Research*, 216: 525–543.